

POLYPLOIDY AND APOMIXIS IN COTONEASTER

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THE ROSACEAE have drawn the attention of investigators because of the variety and beauty of their flowers and fruits as well as their horticultural value. They are a large and varied family with a wide distribution. Many examples of polyploidy and apomixis have been reported in this family.

Of the four subfamilies of the Rosaceae, the Pomoideae are of special interest because of their allopolyploid origin. The basic chromosome numbers of the other subfamilies, the Rosoideae, Prunoideae and Spiroideae, are 7, 8, and 9. The basic chromosome number of the Pomoideae is 17, derived from primitive ancestors by hybridization followed by chromosome doubling.

The eighteen genera of the Pomoideae are rather closely related, as is shown by the fact that many generic hybrids occur in nature. Their close relationships are further supported by the readiness with which most of the genera can be intergrafted.

Many of the genera of the Pomoideae are characterized by secondary polyploidy, that is, the chromosome number in many cases has doubled again, this time probably by autopolyploidy. Secondary polyploidy is common in *Malus* and *Crataegus*.

The genus *Cotoneaster* is less well known than *Malus* and *Crataegus* of the same subfamily. In his "Manual of Cultivated Trees and Shrubs" Rehder (56) notes that there are about 50 species of *Cotoneaster* in the temperate regions of Europe, N. Africa and Asia (except Japan, where there are no native species). These are mostly shrubs, rarely small trees, with some beautiful prostrate forms among them. Their fruit is especially attractive: red, black, purple and a few orange pomes. They are planted often because of their brightly colored fruits as well as the flowers, which are in many cases small, white to pinkish and of many-flowered corymbs. There are also some evergreen and partly evergreen varieties, both upright and prostrate forms, which are very beautiful with the brilliantly colored fruit.

Plant collectors have brought many species of these Cotoneasters into cultivation. Their size, variety, and adaptive qualities make them desirable as ornamental plants. The relationship of these species is not very easily determined, and the Cotoneasters have been considered a difficult genus by the taxonomist.

The characteristics often show differences in size, hairiness, etc., but mostly intensification of some character predominating over that in another species, and often that is the only difference. In reading over the descriptions of the many species and varieties, as well as observing them

in the field, it becomes apparent why *Cotoneaster* is a difficult genus for the taxonomist. In describing *C. francheti* var. *sterneana*, W. B. Turrill (74) in 1950 remarks, "While we have not sufficient information to give full reason for this, since we do not know how far hybridization happens in the wild, how plastic are individual plants, or how much intraspecific genetic variations occur, there results frequent difference of opinion between 'lumpers' and 'splitters.' Splitters have been carried too much." He cites *Crataegus* and appeals to the cytogeneticist to study *Cotoneaster*.

POLYPLOIDY AND APOMIXIS IN THE ROSACEAE

Doubling of the chromosome number at the time of union of the egg and male nuclei followed by a reduction to half the number at the time the spore mother cells divide to form the megaspores and microspores is general throughout the plant kingdom. Asexual methods, such as root or stem cuttings, leaf and axillary bulbs, budding, etc., also occur, but these do not involve a doubling and reduction of the chromosome number; the offshoot carries the chromosome number of the organ from which it comes, while in sexual reproduction there is an alternating cycle between the haploid and the diploid number of chromosomes.

Many instances of changes, modifications of the usual behavior, or abnormalities have been found to occur in the development of the egg and male nuclei and in the development of the spores to form the gametophytes which produce the eggs and the male nuclei. Some of these, such as the functioning of a cell or cells of the integument of the ovary to form the embryo, or the direct development of a megaspore mother cell without reduction to form the spores, the development of an unreduced egg cell, do not involve a change in the chromosome number. These various substitutions for fertilization and meiosis are classified under the term apomixis. Parthenogenesis, apospory, apogamy, and vegetative buds are all included.

No attempt will be made to review all the literature on the subject of apomixis. The earlier work has been reviewed by several investigators, Ernst, 1918 (16) and others including Rosenberg (58) in 1930, who gave a summary of the work up to that time. Steil in 1939 (70) reviewed the literature on ferns. Then Stebbins (68) brought the review up to 1941 in his discussion on "Apomixis in the Angiosperms." The subject again underwent a thorough review by Gustafsson (31) in 1947. Subsequently many instances of apomixis have been reported, especially in connection with polyploidy. This work, as well as the extensive literature on polyploidy, will be discussed here only in connection with the work on the Rosaceae, of which *Cotoneaster* is a member.

The role of polyploidy and apomixis in speciation, evolution and geographical distribution is well illustrated in many genera of the Rosaceae. In general there is much variation in the appearance of apomixis and a relatively high frequency of polyploidy.

Much of the early work on polyploidy in relation to speciation was done

with the genus *Rosa* by Blackburn and Harrison (4) in 1921, Täckhohn (71) in 1922, and Hurst (36, 37, 38) in 1925, 1928, and 1932. A wide range of polyploidy was found, and Hurst attempted to classify the species of *Rosa* into five basic genomes. Crosses between the basic diploid species gave rise to the complexities of the polyploid species. Later cytological studies of this same group by Gustafsson and Häkensson (32) and Gustafsson (29) gave further information indicating that the cytogenetic relationships of the *Rosa* species are more complex with both auto- and allopolyploid as well as intermediate complexes. Fagerlind (18, 20) goes even further and suggests that segmental interchange between the chromosomes of the basic genomes leads to complex pairing relationships in triploids. Both Gustafsson and Fagerlind concluded that apomixis in *Rosa* was a species trait present in diploid species, and that the present association between polyploidy and apomixis is secondary.

Many of the North American species of *Rubus* were found to hybridize by Brainerd and Peiterson (5) in 1920 and Peiterson (52) in 1921. In the experiments, hybrids between different sexual species of *Rubus* (Peiterson, 52) and other genera have in no instances shown any clear indication of apomictic reproduction, even though the parental species are closely related to apomictic forms. Longley (43) in 1924 suggested that apomictic forms existed. In 1930 Gustafsson (25) reported unreduced pseudogamy in a species of *Rubus*. In some cases of pseudogamy the number of apomictic and sexual offspring vary according to the chromosome number of the pollen parent. Darrow and Waldo (11) 1933, reported that the fertilization of a tetraploid species of *Rubus* with pollen from a diploid species yielded a majority of sexual offspring; but it and other tetraploid apomicts produced few or none with pollen from tetraploid species. Crane (7) obtained similar results when using pollen from a diploid form of *R. idaeus* on an octaploid species of *R. vitifolius*; only pentaploid hybrids were produced. When he used pollen from the tetraploid form of the same parent, hybrids and matriclinous octoploid offspring resulted. Pollen from the hexaploid *R. loganobaccus* ($2n = 42$) produced only hybrids. Petrov (53), using pollen of the hexaploid *R. loganobaccus* on a triploid with unreduced eggs, obtained hexaploid hybrids; but using pollen of a triploid, *R. idaeus*, only triploid pseudogamous progeny result.

Although polyploidy is common in the genus *Rubus*, Gustafsson (27, 28) found apomixis was confined to only one section. As in *Rosa*, many of the species are facultative apomicts.

Many of the facultative apomicts are heterozygous, and Haskell (34), 1953, has suggested that another factor in the variation of *Rubus* may be crossing over at meiosis in the production of an unreduced egg cell. In *Rubus* crosses between two facultative apomicts give sexual progeny.

The genus *Potentilla* has also provided evidence regarding the role of polyploidy in evolution and speciation (Claussen, Keck and Hiesey 6), 1940, and the role of apomixis. *Potentilla* species (Müntzing 46 and 47) showed variation in the development of the microspore mother cell. Meio-

sis was regular in the microspore mother cell of *P. argentea* but irregular in *P. collina* and *P. hirta*. *Potentilla argentea* is apomictic through facultative apospory. The embryo may develop autonomously. Similar results were reported by Popoff (55), Gentcheff (23) and Gentcheff and Gustafsson (24). The genetic studies of Müntzing and Müntzing (49) on reproduction between sexual and apomictic forms indicate that apomixis is controlled by multiple factors.

Among the Prunoideae the genus *Prunus* has been studied extensively. Meurman (45) in 1929 reported a high polyploid species, *Prunus laurocerasus* L. with eighty-eight chromosomes. Polyploidy is common in *Prunus*, and the allopolyploid origin of *P. domestica* was determined by Rybin (59) in 1936. According to Almeida (1), *P. lusitanica* is an octopolyploid with $2n = 64$, an allopolyploid of ancient origin behaving like a diploid. Cytological work by Schelhorn (65) showed great irregularity in the nuclear divisions and tetrad formation in a triploid of *P. avium*, which the author believes arose by the fertilization of an unreduced sexual cell of *P. avium* with a sexual cell, and not as a cross of *P. avium* and *P. cerasus*.

The basic diploids show considerable stability of the genome, as is evidenced by the regular meiosis and high fertility of the hybrid between *P. tomentosa* from China and *P. besseyi* from Central North America (Sax unpublished). Apomixis has not been found in this subfamily.

Little cytological work has been done on the Spiroideae, but both autopolyploidy and allopolyploidy have been found in *Spiraea*, Sax (64). Polyploidy appears to be related to geographical distribution, since the Old-World species are largely diploid while most of the American species are late-flowering tetraploids.

The Pomoideae are unique in that the subfamily is of allopolyploid origin. Secondary polyploidy is common in most of the genera, and triploids play an important role in both natural and cultivated species. Polyploidy has complicated the genetic and taxonomic variation of most of the genera and in a few cases is related to geographic distribution.

The first extensive work on the genera of Pomoideae was done by Longley (42) in 1924. He determined the chromosome number in eighty species of *Crataegus* from the collection in the Arnold Arboretum. He found thirteen diploids, sixty-seven triploids, and ten tetraploids.

The chromosome relationship in the Pomoideae was studied by Sax (62 and 63). In the Rosaceae the subfamilies, the Rosoideae, Prunoideae and Spiroideae, have basic chromosome numbers 7, 8 and 9, while the Pomoideae have 17 as the basic chromosome number. The close relationship among them suggests that they originated as a cross between primitive ancestors of the other Rosaceae.

Dermen (12) in 1936 discovered in *Malus hupehensis* a delayed development of the embryo from the unreduced egg after the flower opened.

Johansson (39) suggested that there were four places of fruit origin: the Caucasian region, the Turkestan region, the East Asiatic region in-

cluding East Siberia, and North America. The new varieties arose through crossing, mutation, and doubling of the chromosome number.

Polyploidy in *Malus* has been studied by several workers. Einset (13, 14) found spontaneous polyploids among apple seedlings. Einset and Inhofa (15) also described periclinal chimeras; partly diploid, partly tetraploid, in apples. Hemming (35) discusses the origin of apples and the relation of diploid, triploid, and tetraploid species.

Some correlation has been shown between geographical distribution and polyploidy. Hägerup (33) in 1931 postulated an increase in the frequency of polyploidy with the increase in latitude. The results of studies by Tischler (73) of the frequency of polyploids at different latitudes in Sicily, Schleswig-Holstein, the Faeroes and Iceland supported that hypothesis. Further corroboration came from Flovik (22) in his investigations of the flora of Spitzbergen, all glacial survivors.

Gustafsson (26), Babcock and Stebbins (2), and Stebbins and Babcock (67) have found apomicts to be excellent material for studying the effect of environment on the genotype and the tracing of plant migrations. The distributional center of the American *Crepis* complex was found in northeastern California. Fernald (21), followed by Babcock and Stebbins (2), also considered the Appalachians to hold the ancient American *Antennaria* complex. Gustafsson (28) has made similar studies of *Taraxacum* and *Rubus* in Scandinavia. Curtis (9) also used apomicts in *Taraxacum* in England for the study of the effect of environment on the genotype.

Other literature on the subject of plant distribution was reviewed by Löve and Löve (44) in their work on "The Geographical Significance of Polyploidy." They conclude that polyploidy increases with the increase in latitude or the extremeness of the Pleistocene or post-glacial climate. The estimated frequency of polyploidy in the temperate zone is 30 per cent or lower.

COTONEASTER

In the present work the chromosome numbers of most of the species in the genus *Cotoneaster* were studied. It was hoped that this would show something concerning the relationships of some of the species, whether or not the species were polyploid, and give evidence as to whether there existed in this genus some of the irregularities in reproduction found in other genera of the Rosaceae as in *Malus* and *Crataegus*.

The presence of apomixis was also tested. Each season the flowers on some of the branches of a few species were destyled and emasculated while in the bud on some of the plants to see if they would produce fruit without fertilization; and if, as has been found in the apples, the development of the embryo could take place independently of fertilization by development from some part of the ovule. There are only a few species in which this work was done. Since only positive results were conclusive because in a few cases no fruit was set on the controls or occasionally on the entire plant, these results will be mentioned in connection with the species.

Seed from some of the species were planted to compare the progeny from the same seed source, to observe their resemblance to the parent plant, and to determine the proportion of hybrid plants occurring in natural populations.

The Cotoneasters in the Arnold Arboretum are all introduced species from Europe, Asia, and Africa. A few of these species were obtained from crosses made in cultivation; others were collected and brought into cultivation. The source of the species was usually known, especially the immediate place from which it was introduced. In most cases the plants came directly from their place of origin. The Arnold Arboretum's own collector, Ernest Wilson (75) brought seeds and plants from Asia directly to the Arnold Arboretum. Many of them bear the authority of Rehder and Wilson. In other cases seeds have come from well-known plant explorers in England, France, Germany, Holland, China, and India, and other equally familiar sources elsewhere and in the United States.

The material for the present work was collected during the spring and summer of the years 1950 through 1954 and was confined to the species available in the Arnold Arboretum. This included most of the well-known species, as may be noted from the list given in the table (Table I), although not all the varieties of each species were studied. There were a few plants labeled "C. sp." denoting the difficulty in naming them, and as mistakes in labeling may occur in the best collections, the number on the metal label on each specimen was copied for further tracing if necessary. All were checked with the specimens in the herbarium of the Arnold Arboretum.

The Cotoneasters blossom over a fairly long period in the spring, but it is necessary to obtain the dividing microspore mother cells at the right stages in division. During a particularly warm day most of the buds on a plant might pass through the division stages. In some species where new buds are produced over a longer period, material is more easily obtained. The difficulties of fixing such a large number of varieties in a short time meant that some were missed some years. In some rare cases the plants were not in flower every year or they were newly planted. The size of the flower bud when the divisions occurred differed in the various species. However, most of the available species, though not all, were obtained when the divisions were in progress each season, and the results were determined and checked. All those reported were checked at least two seasons, and many were studied four or five seasons.

The buds were fixed in alcohol acetic solution twenty-four hours, then changed to 95% alcohol. These were left under refrigeration until acetocarmine smears of the pollen mother cells could be made and studied.

The chromosomes in the Cotoneasters are small, but there was an abundance of material and in practically all cases it was possible to obtain well-fixed material at all stages.

In the study of the chromosome numbers it was noticeable that the chromosome pairing was quite characteristic for any given species. In many of the species there was a tendency for the sets of chromosomes to

adhere strongly in the late prophase and metaphase, and at these stages in many cases the count would be 17 or thereabout even when the form was triploid or tetraploid except for a few univalents. The chromosomes in these cases would appear unusually large for *Cotoneaster*. However, as the chromosomes separated and were counted in the anaphase stage, it was apparent that the species were often triploid or even tetraploid.

The diploids are very regular in their divisions. The 17 small chromosomes pass to the poles and are easily counted. The polyploids were not so easily counted in all cases, but they had a very characteristic appearance. The chromosome complex was larger and the pollen mother cells were usually so much larger that they suggested polyploidy after one became familiar with them. This did vary somewhat, but in all the diploids studied the pollen mother cells were smaller than in most polyploids; exceptions were noted in the polyploids.

Univalents were very often present in the dividing nuclei of the polyploids. The triploids showed chromosome bridges and other irregularities. The chromosome count varied according to the closeness of adherence of homologous pairs. Often pieces of chromatin, even whole chromosome bridges were left outside in the cytoplasm. As many as twelve such chromosome remnants were counted, but usually two to six were found outside in the cytoplasm. These were visible after the daughter nuclei had rounded up in the later stages. Tetraploids were less irregular, although univalents were often present. The number was obviously larger, and when they separated the counts showed the tetraploid number. At time some of the univalents were lost in the cytoplasm.

The counting of the chromosomes in the polyploids is complicated by an early loosening of the arms of the V-shaped chromosomes as they near the poles, which makes it appear as a larger number of chromosomes if the two arms are counted separately.

In every species the counts were checked from the same slides by Professor Karl Sax, to whom I wish to express my thanks.

The results of these studies are given in Table I. The species are listed in alphabetical order.

TABLE I
COTONEASTER

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. acuminata</i> Lindl. 226-39 *	Himalayas	5	2 n
<i>C. acutifolia</i> Turcz. 15686	N. China	4	2 n
<i>C. acutifolia</i> ? 2291	Tao Basin		3 n
<i>C. acutifolia</i> var. <i>villosula</i> Rehd. & Wils. 13165B	Cent. & W. China	5	4 n

* Numbers refer to Arnold Arboretum accession numbers.

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. adpressa</i> Bois 7951	W. China	4	3 n
<i>C. adpressa hessei</i> 813-41			3 n
<i>C. adpressa</i> var. <i>praecox</i> (Vilm.) Bois & Berthault. 134-18			3 n
<i>C. affinis</i> var. <i>bacillaris</i> (Lindl.) Schneid. 17806-A & B	Himalayas	7	4 n
<i>C. ambigua</i> Rehd. & Wils. 134-22	W. China	5	3 n
<i>C. apiculata</i> Rehd. & Wils. 7275	W. China	4	3 n
<i>C. bullata</i> Bois 861-32A	W. China	5	3 n
<i>C. bullata</i> f. <i>floribunda</i> (Stapf) Rehd. & Wils. 6685-2	W. China		3 n
<i>C. bullata</i> var. <i>macrophylla</i> Rehd. & Wils. 13426	W. China		3 n
<i>C. conspicua</i> Marquand 1019-36C	W. China	7 ?	2 n
<i>C. dammeri</i> Schneid. 137-51	Cent. China	5 ?	2 n
<i>C. dielsiana</i> Pritz. 686-33	Cent. & W. China	5	3 n
<i>C. dielsiana</i> Pritz. 134-28A & B			3 n
<i>C. divaricata</i> Rehd. & Wils. 6587C	Cent. & W. China	5	3 n
<i>C. foveolata</i> Rehd. & Wils. 13431A & B	Cent. China	4	3 n
<i>C. francheti</i> Bois 130-32D	W. China	6 ?	4 n
<i>C. frigida</i> ? Lindl. 191-40	Himalayas	7	2 n
<i>C. froebelli</i> Vilmorin 757-30B	Cult.		3 n
<i>C. glabrata</i> Rehd. & Wils.	W. China	7	2 n
<i>C. glaucophylla</i> Franch. 571-36	W. China	7 ?	3 n
<i>C. henryana</i> Rehd. & Wils. 223-07	Cent. China	7 ?	2 n
<i>C. horizontalis</i> Decne. 45-34	W. China	4	3 n
<i>C. horizontalis</i> var. <i>perpusilla</i> Schneid. 7157A	W. China		3 n
<i>C. horizontalis</i> var. <i>prostrata</i> 1070-38			3 n
<i>C. integerrima</i> Med. 1776-3, 1766B	Europe, N. Asia to Altai	5	3 n
<i>C. lindleyi</i> Steud. 372-37-A	Himalayas	6 ?	3 n
<i>C. lucida</i> Schlecht. 3284A & B	N. China, Mongolia Altai Mts.	4	3 n
<i>C. melanocarpa</i> Lodd. 6679-1	Europe to Cent. & N.E. Asia	4	4 n
<i>C. melanocarpa</i> var. <i>commixta</i> Schneid. 656-33			4 n ?
<i>C. melanocarpa</i> var. <i>laxiflora</i> (Lindl.) Schneid. 13490-1A	Cent. Asia		3 n
<i>C. microphylla</i> Lindl. 22906	Himalayas	5	2 n
<i>C. moupinensis</i> Franch. 13497A & B	W. China	6 ?	3 n
<i>C. multiflora</i> Bge. 21976, 14916	W. China	5	4 n

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. multiflora</i> var. <i>calocarpa</i> Rehd. & Wils. 6679-1 & 2	W. China		3 n ?
<i>C. multiflora</i> var. <i>granatensis</i> (Boiss.) Wenz.	Spain	6	3 n
<i>C. nitens</i> Rehd. & Wils. 6681	W. China	4	3 n
<i>C. obscura</i> Rehd. & Wils. 6686-1	W. China	5	3 n
<i>C. obscura</i> var. <i>cornifolia</i> Rehd. & Wils. 11261A & B	W. China		3 n
<i>C. racemiflora</i> var. <i>desfontaini</i> (Reg.) Zab. 389-34	S. Eur., N. Afr., W. Asia to Himalayas and Turkestan	4	3 n
<i>C. racemiflora</i> var. <i>soongorica</i> (Reg. & Herd.) Schneid. 16428, 21846	W. China	3	3 n, 4 n
<i>C. racemiflora</i> var. <i>veitchii</i> Rehd. & Wils. 20075	Cent. China		3 n
<i>C. rosea</i> Edgew. 44939	N.W. Himalayas, Afghanistan	5	3 n
<i>C. rotundifolia</i> Lindl. 405-36A	Himalayas	6 ?	3 n
<i>C. rubens</i> W. W. Sm. 21991B	W. China	6 ?	3 n
<i>C. salicifolia</i> Franch. 434-33A	W. China	6 ?	
<i>C. salicifolia</i> var. <i>rugosa</i> (Pritz.) Rehd. & Wils. 458-36-A	Cent. China	5	3 n
<i>C. schneideri</i> 574-38-B			4 n
<i>C. simonsii</i> Bak. 596-33	N.W. India, Khasia	5	3 n
<i>C. sp.</i> H. Hesse 13492			3 n
<i>C. sp.</i> 524-30A & B			3 n
<i>C. sp.</i> 114-36B	China (Lu Shan Arb.)		3 n
<i>C. tenuipes</i> Rehd. & Wils. 7276A-C	W. China	5	3 n
<i>C. tomentosa</i> (Ait.) Lindl. 23-42-4A, 13507-1	S.E. Europe, W. Asia	4	3 n
<i>C. wardii</i> W. W. Sm. 659-33	S.E. Tibet	7 ?	3 n
<i>C. zabeli</i> Schneid. 7019B	Cent. China	4	3 n
<i>C. zabeli</i> var. <i>miniata</i> Rehd. & Wils. 7343D, 156-85	China		3 n

Triploid and tetraploid *Cotoneasters* are apt to be more vigorous than the diploids — but there is much variation among these; some are less vigorous. Often the main differences given in Rehder's Manual between some of the species and varieties is in vigor, intensity of color, size of flowers, leaves and fruit, pubescence, or looseness of inflorescence. There are other differences between species, but these are much the same variations existing between known diploid and triploid or polyploid species derived from them.

Cotoneaster acuminata Wallich is one of the first species described (Flora, 1823). It is a diploid species from Zone 5 in Nepalia in the

Himalayas (Table I.) A natural hybrid between this species and *C. acuminata* was collected by R. N. Parker. *Cotoneaster acuminata* is found along the Himalayas to Calcutta.

According to the table (Table I) the chromosome count for *Cotoneaster acutifolia* Turcz. is 17. The pollen mother cells were small. It is a diploid and its natural habitat is N. China. It has been found on a mountain near Peking by Bretschneider. Specimens in the herbarium from various localities in northwest China at high altitudes are labeled *C. acutifolia* Turcz. Wilson (75) says there is no typical *acutifolia* in China proper, but in Mongolia, but that there are two well-marked varieties in central and west China.

Another plant labeled *C. acutifolia* (?), carrying a different number, was grown from seed collected by Joseph F. Rock in the Tao River Basin, Kansu Province, China. It is obviously a different variety with a triploid chromosome count and lagging chromosomes. This is a triploid probably derived from *C. acutifolia* Turcz.

One of the varieties, *C. acutifolia* var. *villosula* Rehd. & Wils., is found in Central and West China. This is a polyploid and was recognized as a new variety by Rehder and Wilson (56). It is described as "densely villous beneath, somewhat larger; calyx tube more densely villous; fruit thinly pubescent." From the chromosome counts this was considered a tetraploid, although there was some irregularity.

Closely related to *C. acutifolia* Turcz. is *C. ambigua* Rehd. & Wils. from West China which, according to Rehder's Manual of Cultivated Trees and Shrubs (56), "differs chiefly in its slightly pubescent or nearly glabrous calyx tube and subglobose fruit with three to four nutlets." *Cotoneaster ambigua* is a coarser plant in general and more rigid in appearance than *C. acutifolia* Turcz. and bears a closer resemblance to *C. acutifolia* var. *villosula* Rehd. & Wils., but on comparison of the two plants side by side in the field they appeared sufficiently different to be separate species. In *Plantae Wilsonianae*, Wilson (75) makes the remark, "In speaking of *ambigua*, it is noted that all *acutifolia* like specimens are grown in the arboretum and later it may be possible to determine their relation to each other." *Cotoneaster ambigua* is a triploid. The divisions of the nucleus in the pollen mother cells are irregular with bridges still holding at anaphase and scattered univalents. The homologues show some tendency to adhere. The pollen mother cells often did not finish dividing but decomposed at some stage in their development. There was also much variation in the stages in an anther and much decomposition in the pollen mother cells. *Cotoneaster ambigua* produced fruit. The specimen in the Arnold Arboretum was heavily fruited in 1953, suggesting apomixis in such an irregular triploid.

Cotoneaster tenuipes Rehd. & Wils. is also noted as a species closely related to *C. acutifolia* Turcz. It has a very graceful fine slender development throughout and would not be mistaken for either *C. acutifolia* var. *villosula* or *C. ambigua*. It is less coarse even than the diploid species *C. acutifolia* Turcz. *Cotoneaster tenuipes* is a triploid form which has smaller

chromosomes and pollen mother cells like those of the diploid, but the chromosome number is higher than the basic number for the genus. There were chromatin bridges and fragments in the cytoplasm at anaphase. Although the pollen grains were smaller, like those of a diploid, it was obviously a triploid or aneuploid. There was little mature fruit on the plant in the years 1950–1952, but it was well fruited in 1953. It is probably apomictic.

Cotoneaster tenuipes Rehd. & Wils. grew in West China, as did *C. ambigua* Rehd. & Wils. and *C. acutifolia* var. *villosula* Rehd. & Wils., the latter extending into central China. The two former are triploids, the latter a tetraploid. They grew in Zone 5 (i.e. Rehder's Map of Climatic Zones), while *C. acutifolia* Turcz. was found in Zone 4 and in North China.

There must be some relationship between them, as they have similarities that the systematist recognizes. There is the possibility that the triploids just mentioned came from a cross in which *C. acutifolia* was one of the parents, or that the chromosome number of *C. acutifolia* had doubled in number, forming a tetraploid (var. *villosula*) and then back-crossed with *C. acutifolia* or another diploid, giving triploids. Their distribution would support this assumption.

Cotoneaster lucida Schlecht. was once labeled *C. acutifolia* Lindl. (not Turcz.). It came from the Altai Mountains in Mongolia, Zone 4 (North China). It is quite different from *C. acutifolia* Turcz. *Cotoneaster lucida* has larger glossy and lustrous leaves. It is a triploid. It may be that this species has some relationship to *C. melanocarpa* as well as *C. acutifolia*.

Cotoneaster foveolata Rehd. & Wils. is represented by two vigorous specimens in the Arboretum grown from the same collection of seeds. They are alike. *Cotoneaster foveolata* is a large stiff shrub with large leaves. It is a triploid with much irregularity in the nuclear divisions of the pollen mother cells. Pieces of chromatin are left out in the cytoplasm after the dividing nuclei are formed. *Cotoneaster foveolata* comes from central China, Zone 4.

Cotoneaster moupinensis Franch. is a large stiff shrub which, like *C. foveolata*, has a rigid appearance. Rehder describes it as "similar to *C. bullata* but with black fruit." It comes from western Szechuan, West China, at 1300–2000 m. altitude. It is common in woods and thickets. It is a triploid. Wilson comments about the series as follows: "It must be confessed, however, that there is a great similarity between all these black fruited *Cotoneasters* from China." He noted that there were only slight variations between these *acutifolia*-like species and that they could be arranged in a gradual series. He believed that since they are all cultivated in the Arnold Arboretum someone may later determine their affinities and find the relations of the *acutifolia*-like ones.

Cotoneaster bullata Bois and its variety *C. bullata* var. *macrophylla* Rehd. & Wils. are among the most attractive shrubs in the Arboretum in the autumn because of their large clusters of abundant brilliant red fruits and very healthy dark green leaves. The *macrophylla* variety is especially

striking, having a larger leaf and inflorescence. Wilson says that *C. bullata* is a comparatively rare plant, though scattered over wide areas in Szechuan. It is found in open conifer forests in southeastern Tibet at 9000–10000 feet, inhabiting Zone 5—a zone adjacent to that of *C. moupinensis*, which is in Zone 6 in that same area. *Cotoneaster bullata* Bois is a triploid. The division of the nuclei of the pollen mother cells was very irregular, with twenty-two to twenty-eight chromosomes, depending on the looseness of pairing. There were chromosome bridges and many univalents, up to as many as twelve in one anaphase.

The variety *C. bullata* var. *macrophylla* Rehd. & Wils. is also a triploid; univalents, bivalents, and trivalents are present. It is very irregular, with chromosome bridges at anaphase.

Another form, *C. bullata* f. *floribunda* (Stapf) Rehd. & Wils. is very attractive. It also has a triploid number with univalents and lagging chromosomes, but its homologues seem to be more closely paired. Under his remarks Rehder includes *C. moupinensis* var. (Stapf) as a synonym. It seems significant that this form *C. bullata* f. *floribunda* was described as *C. moupinensis* var. Stapf. It has bright red berries. *Cotoneaster bullata* f. *floribunda* is also found in the thickets of Szechuan, China. It is possible that *C. bullata* and varieties came from similar parental ancestry as *C. moupinensis*.

Very bright red berries with intensely green foliage and an attractive low habit characterize *C. apiculata* Rehd. & Wils., which grows in West China. This is a triploid with chromosome bridges and other irregularities in the reduction divisions in the anthers. In the late anaphase there are chromosome fragments left in the cytoplasm. Rehder gives *C. apiculata* as nearly related to *C. disticha* Lange, which ranges from the Himalayas to southwest China. (The latter was not in the Arboretum collection except for small cuttings, and it is not included in the counts. Counts on leaf-tip smears show that it is not a diploid.) There were three plants of *C. apiculata* grown from seed collected from the type plant by Wilson in China. They were alike. George Graves raised twenty-five plants from seed collected in the Arboretum. All were alike. The same was true of twenty-nine seedlings grown in the greenhouse, making a total of fifty-seven seedlings from the same original source.

Cotoneaster Lindleyi Steud. is a triploid. It produced no fruit 1950–1952, although it had some flowers on it in 1950 and 1951. In 1953 it flowered abundantly and produced fruit. This fruit became a deep lavender or bluish purple as it developed (much like that of *C. affinis* var. *bacillaris*) and gradually turned a purple brown and finally black—a word used by Rehder. Rehder includes *C. Lindleyi* as a species closely related to *C. racemiflora* (Desf.) K. Koch. It is a conspicuous species with its broad oval to broad ovate leaves rounded at the base. It came from the Himalayas (Rehder, Zone 6). It was very susceptible to fire blight.

Cotoneaster affinis var. *bacillaris* (Lindl.) Schneid. is probably a tetraploid. There were seventeen large tetravalent chromosomes in early equa-

torial plate stage and double that number at anaphase. Like *C. affinis* Lindl., which is not in the Arboretum, it is said by Rehder (56) to be closely related to *C. frigida*.

Cotoneaster frigida Lindl. is a diploid having seventeen chromosomes. Our specimen of *C. frigida* is quite different from the upright type described as typical. It lies flat on the ground with branches very stiff, like the one collected at Darjeeling. Some fruit set on the two destyled branches. The fruit is large and of a bright red color quite unlike that of *C. affinis bacillaris*. The latter is found in the Himalayas, as is *C. frigida*. They grow in Zone 7 (Rehder).

It is probable that *C. affinis* var. *bacillaris* came from the doubling of the chromosome number in *C. frigida* or a cross between *C. frigida* and some other form. There is quite a noticeable similarity between *C. affinis* var. *bacillaris* and *C. lindleyi*, which is a triploid. *Cotoneaster lindleyi* may have come as a backcross from *C. affinis* var. *bacillaris* and a diploid. There are several diploids in that region.

In writing of the variety *C. dielsiana* var. *elegans* Rehd. & Wils., Wilson remarks on the herbarium sheet that "this western plant shows marked differences from the type . . . in several respects approaching *francheti* Bois. It also has affinity with *C. Zabeli* Schneider. Its thinner yet more persistent leaves, smaller pendulous fruit, brick and orange red, distinguish this variety from the typical form." It is found in thickets 3500–4000 feet on the eastern slope of Likiang snow range, Yangtze Watershed, Szechuan. These observations are supported by a study of the chromosomes.

There are three specimens of *C. dielsiana* Pritz. in the Arboretum. One (*C. dielsiana* 686–33) was from the United States Department of Agriculture. After *C. dielsiana* was fixed two years in succession, a difference in the behavior of the chromosomes was noted for the two years. A check of the numbers showed that the material had come from the other two plants the second year. These two plants were grown from seeds labeled *C. dielsiana* 134–28–A & B, which were collected by Wilson in China, and they are alike. The fruit of this specimen is red and waxy and the leaves have color in the fall. It fits the description by Rehder. The fruit of the U. S. D. A. specimen is a reddish yellow fruit like that described for the variety *elegans*. *Cotoneaster dielsiana* (686–33) varied in the chromosome counts, depending on the looseness of pairing of the homologues. There were univalents, bivalents, and trivalents. Bridges were present in the anaphase stage. This is undoubtedly a triploid.

The chromosome counts from the specimens grown from the seed from China (134–28) appear to be 17 and up to about 21 in equatorial plate stage, depending on looseness of adherence. In the first anaphase the count appears to be higher than it appears at metaphase, and univalents and stragglers are apparent. The second anaphase counts are 17 and higher with irregularities. This may be an aneuploid.

George Graves grew a thousand seedlings from seed collected in the Arnold Arboretum. They were uniform in habit and growth like the 673

seedlings from 134–28 grown in the greenhouse. They are undoubtedly apomicts, as there were many kinds of Cotoneasters growing near by.

There were five specimens of *C. divaricata* Rehd. & Wils. growing from a collection of seeds from China. There were no discernible differences between these. George Graves grew two hundred seedlings of *C. divaricata*. They showed no variation.

Cotoneaster divaricata is a triploid species with lagging chromosomes and univalents. It is very probably an apomictic triploid.

There are several varietal forms of *C. racemiflora* (Desf.) K. Koch (in the Arnold Arboretum) which are quite widely distributed in their origins and show much variation. They are found in southern Europe, North Africa, western Asia to the Himalayas and Turkestan. *Cotoneaster racemiflora* (Desf.) K. Koch is described by Rehder (56) as “a variable species, the typical form variety *C. racemiflora* var. *desfontaini* (Reg.) Zab. (var. *typica* Schneid.) has generally elliptic acutish leaves, while variety *nummularia* Dipp. has broader usually obtuse leaves.”

The divisions of the nucleus of the pollen mother cells in *C. racemiflora* var. *desfontaini* (Reg.) Zab. are fairly stable in appearance, but there are some univalents and bridges in both divisions and some chromatin left out after the daughter nuclei are formed. The pollen mother cells and the chromosomes are large for the genus and the chromosome count shows that it is polyploid, probably a triploid, the homologues pairing loosely.

Some fruit set on the destyled pistils in *C. racemiflora* var. *desfontaini*, but only on some of the destyled branches. However, when set, the fruit was abundant on the destyled branches as well as on the controls.

Cotoneaster racemiflora var. *soongorica* (Reg. & Herd.) Schneid. from West China is represented in the Arboretum by two plants from different sources. They are growing side by side. The fruit of one, which came from the Framingham Nurseries, is a little darker in color, maturing a little later than the other, which was grown from seed (Hort. Judd). They both appear to be triploids, but there are some differences in their chromosome behavior. In the plant raised from seed there appeared to be a higher chromosome number. Perhaps the homologues were more easily separated. One of the obvious phenomena noticed in both cases — but especially in the plant from the nursery — was the large number of examples of the stages where the homologues were pulled apart along the plate but still adhering. The whole complex would be in that condition with several univalents and bivalents less regularly placed.

Cotoneaster racemiflora var. *veitchii* Rehd. & Wils. from Central China possessed the number of chromosomes and the irregularities of a triploid.

Cotoneaster rosea, another triploid, has attractive small pink flowers in glabrous three- to nine-flowered cymes. It comes from the northwestern Himalayas and Afghanistan. It is probably a facultative apomict, as it hybridizes at times with *C. acuminata*, according to Parker's notes on the herbarium sheet. Its branches are slender. It is supposed to be related to *C. racemiflora*, as shown especially by its fruit.

Cotoneaster multiflora Bge. is a very graceful shrub from western

Szechuan. It is handsome in bloom and it has attractive red fruits. This is a tetraploid. The counts are around 34. Late anaphase shows a larger count, which is characteristic, as the two arms of the chromosome separate further in the reorganization of the daughter nuclei. The divisions are fairly regular. Although *C. multiflora* grows in West China, the Arnold Arboretum Herbarium has also a specimen from Kashmir. This may be a variety of *C. multiflora* or of *C. racemiflora*.

Cotoneaster multiflora var. *calocarpa* Rehd. & Wils., with rosy-colored blossoms, shows much irregularity. It is probably a triploid, although at times it appeared to have too many chromosomes. They may be the homologues prematurely separated.

Cotoneaster multiflora var. *granatensis* (Bois.) Wenz. is a triploid, the chromosome counts varying with many univalents — as many as fifteen in one case. The homologues varied in the ease with which they separated. In some cases the division went no further than the pollen mother cells. There was much sterility. The pollen mother cells, as well as the chromosomes, were large.

Among the unidentified species *Cotoneaster* sp. Hesse 13492G is a triploid. The two unnamed specimens collected by Dr. Rock are also triploids. They are alike and came from the same collection of seeds.

It was found that two collections labeled *C. obscura* and collected at different times yielded different results as far as behavior of chromosomes was concerned. One of these gave results similar to those obtained from the material labeled *C. obscura* var. *cornifolia*. A survey of these specimens in the field showed the two latter to be similar, and a checking of the numbers carried by these shrubs against the cards in the files disclosed that the plants had come from the same collection of seeds! (The large label on the questionable plant had omitted the varietal name.) *Cotoneaster obscura* var. *cornifolia* Rehd. & Wils. is a triploid, as it is very irregular with univalents, lagging chromosomes, and irregular pollen size. *Cotoneaster obscura* is also a triploid, but it has fewer chromosomes and is somewhat less irregular in its divisions. The homologues may adhere more closely or it may be an aneuploid. It is not as coarse in general, having smaller leaves, more delicate branches, and dark red fruit, while the variety *cornifolia* has a purple-black fruit. These are both from West China. They are probably apomictic triploids related to *C. acutifolia* or a cross between *C. acutifolia* var. *villosula* and some diploid.

Cotoneaster francheti Bois and *C. schneideri* appear to be identical or nearly so. The appearance and behavior of the chromosomes first called my attention to the similarity. When the plants were checked in the field, they were almost identical. The red fruit of *C. francheti* Bois was a bit more deeply colored than that in *C. schneideri* which was orange-red. The latter, however, although located near by, is more shaded by other plants. It could, of course, be an apomict which is a "clonal variety" with very slight differences. Rehder (56) does not mention *C. schneideri*. The plant in the Arnold Arboretum came as seed from California. *Cotoneaster francheti* is a tetraploid species. It comes from West China.

Rehder comments on the similarity between *C. francheti* Bois. and *C. wardii* W. W. Sm. The leaves of *C. wardii* are larger and in general the bush is more vigorous. It looks quite different. The fruit is larger and red without the orange-red tint noticeable in the red of *C. francheti*. The chromosome behavior is different. *Cotoneaster wardii* is a triploid, probably with *C. francheti* as a parent. This may be a case where the triploid is more pronounced in various ways than the tetraploid.

Two plants of *C. simonsii* in the Arboretum come from different sources; one from seed from Wageningen, Holland, the other as a plant from a nursery. They are not exactly alike in chromosome behavior, one being more irregular with long bridges stretching from pole to pole in the anaphase and with many univalents. The other is a little less irregular, but the chromosome count is the same. Both are triploids according to chromosome count and behavior. The plants vary somewhat, too. The fruits of one are almost always solitary or in a small cyme; the other fruits are in a cyme. The one with solitary fruits is much like the variety *newryensis*, nearly related to *C. francheti*. A total of 384 seedlings of *C. simonsii* gave three variants.

Cotoneaster zabeli Schneid. is represented by four specimens — all from the same collection of seeds. They are alike. *Cotoneaster zabeli* is a triploid. In the third year of the experiment fruit was borne on the destyled branch.

Cotoneaster zabeli var. *miniata* Rehd. & Wils. is a smaller, more delicate variety in habit and flower, with a light orange-scarlet fruit instead of the bright red borne by *C. zabeli*. It is also a triploid. This, like *C. tenuipes*, was expected to be a diploid. It may be an aneuploid, as the count is low for a triploid.

Cotoneaster tomentosa (Ait.) Lindl. is represented by two plants in the Arboretum. They are alike. Each year the flowers on several branches were destyled while in the bud. These set fruit in about the same proportion as on the controls. Apomixis is very definitely shown here. These plants continue to flower all summer up to frost time; only a few flowers are in blossom on each branch at a time. *Cotoneaster tomentosa* is a triploid.

Rehder (56) speaks of *C. tomentosa* being similar to *C. integerrima*, but larger in every part and more pubescent. *Cotoneaster tomentosa* is distributed throughout Europe and West Asia in Zone 4 (Rehder).

One specimen is reported from Kansu, but it may differ and should be compared, as no other report of that kind is made. Two new specimens from a nursery labeled *C. tomentosa* are not like the older *C. tomentosa* planted here, but are more like *C. integerrima*, but larger.

It was noted above that two plants of *C. obscura* var. *cornifolia* Rehd. & Wils. coming from the same seed source were alike in every way, the chromosomes being similar in number and appearance. Several other groups of two or more specimens from the same collection of seeds from a species were growing in the Arboretum. In all these cases plants from the same seed sources were alike. The number was not large enough in

each case to be certain if this was always true for these species, but *Cotoneasters* in general were considered to come true from seeds.

In the behavior of the chromosomes definite groupings are suggested, and a few of these species are very close together. For instance, *C. francheti* and *C. schneideri* are similar, as are the two so closely related *soongoricas*. A note with one specimen of *C. francheti* in the cultivated group describes the fruit as orange-scarlet. Schneider collected an orange-scarlet-fruited specimen at Gotha. Perhaps this is where the name *C. schneideri* became attached to and substituted for *C. francheti* for the California plant, as *C. schneideri* does show a slightly more orange tint. At any rate, *C. francheti* is a tetraploid which shows a deep orange red as it is ripening, and only a slight variation could be the cause of the differences in both cases. *Cotoneaster wardii*, a related triploid, lacks the orange tint altogether. *Cotoneaster francheti* is a tetraploid, which explains to some extent the "splitters" that Turrill mentions in connection with the variety "*sterniana*" and which turns up in *C. schneideri*. Crosses with other species may help to produce the triploids found in cases like *C. wardii*, *C. nitens*, *C. divaricata*, and others.

REPRODUCTION IN COTONEASTER

Most of the *Cotoneasters* have long been known to breed true from seeds. This has been shown by the uniformity in the seedlings grown from the collections of Wilson and others, and frequent mention of the fact that certain species of *Cotoneaster* could be propagated by seeds. Saunders (60), in *Refugium Botanicum*, mentions that *C. buxifolia* comes true from seeds, and gives a list of *Cotoneasters* that may be propagated by seeds. Conrad Loddiges & Sons (41) describe *C. affinis* and *C. melancarpa* as raised from seeds. According to Stapf's (66) description of *C. bullata* in the *Botanical Magazine*, 1909, it produces an abundant crop of seeds to increase the plant.

In the literature on *Cotoneaster* several cases of natural crosses have been reported. *Cotoneaster frigida* Lindl. is of interest in this respect. It has been mentioned as one of the parents in several instances.

Exell (17) collected seeds from a plant of *C. frigida* growing in close proximity to other species of *Cotoneaster* and planted them. Among the resulting seedlings there were six hybrids; the remaining plants were like *C. frigida*. *Cotoneaster watereri* Exell was considered an interesting hybrid between *C. frigida* Lindl. and *C. henryana* Rehd. & Wils. (*C. rugosa* Pritzel and Diels.). *Cotoneaster frigida* Lindl. and *C. pannosa* Franch. gave rise to *C. crispii* Exell. The others were not of horticultural interest.

A. A. Pettigrew (54) of Cardiff obtained seeds of a *C. frigida fructiluteo* plant from Stevenstone, Devonshire. This plant differed from the type in color of the fruit only, which was yellowish or creamy white instead of red. After several years of genetic experiments, on which the final report was not available, the author found red to be dominant, and

he believed that the individual plants of *C. frigida* were self-sterile and that they were fertilized by a red-fruited variety growing in the vicinity.

Conrad Loddiges & Sons (41), in describing *C. frigida*, mention that it should be budded on white thorn stock.

Another instance of the tendency of *C. frigida* to hybridize is the announcement, in *Gardeners' Chronicle* 132: 243, of *C. cornubia* — a hybrid between *C. frigida* and an unrecorded species — as a vigorous plant by Mr. Lionel de Rothschild in 1933. This received an award of merit.

Others report *C. frigida* as breeding true. A. T. Johnson (40) describes *C. frigida* as naturally a free and robust tree "so readily raised from seeds." He also mentions the distinct form *fructo-luteo*. Four seedlings of *C. frigida montana* grown from seed obtained by Donald Wyman from North Africa were alike.

On a note with a specimen from the Flora of Chumbi in the Arnold Arboretum Herbarium, mention is made of the fact that seedlings of *C. frigida* Lindl. are alike; also that seedlings of *C. aldenhamensis* are all alike but not so broad-leaved as those of *frigida*.

R. N. Parker, while collecting in Khadrula India Sikkum, Himalayas, at an altitude of 2700 meters, June 18, 1928, found in a thicket a specimen which he considered a cross (*C. acuminata* Lindl. and *C. rosea* Edgew.). There is a specimen of this in the Arnold Arboretum Herbarium. This has the habit of *C. acuminata* and the pink flowers of *C. rosea*. A plant of *C. rosea* was growing near by the thicket of *C. acuminata* where this hybrid plant was found.

Caution against raising plants from seeds comes from several sources, concerning both the *microphylla* and *salicifolia* groups. Of the probable hybridization in the several species allied to *C. microphylla*, *C. congesta* (Syn. *C. microphylla* var. *gracilis*), and *C. thymifolia* Arthur Osborn (51) writes, "It is best to propagate these distinct forms by cuttings or layers. They do not come true. At least that is our experience at Kew, though this may be due to cross pollination as all are growing in close proximity." W. J. Bean (3) made similar observations, as was noted earlier. The group of species, all natives of the upper and middle basin of the Yangtze River, in which are included *C. salicifolia* and its varieties, *C. glabrata*, *C. henryana*, and *C. rhytidophylla*, have also been reported (66) to hybridize easily. *Cotoneaster watereri* is supposed to have one parent in this group.

The instances of hybridization are few and limited to species or groups where few specific data are available. In an isolated population a species would be expected to breed true, but when numerous species are growing in close proximity variation would be expected. Some cases have been cited where a small number of offspring from the same seed source are alike when species overlap and hybridization could result. The most critical test, however, is the study of the progeny of species grown in a botanical garden where many species are grown in close proximity.

In the Arnold Arboretum most of the species are grown in close proximity, and the time of flowering is essentially the same in some species

and overlapping in others. There is ample opportunity for cross-pollination, since the bees at blossoming time are so abundant that it is difficult to work with the plants.

In order to determine whether most of the species breed true from seeds where there was so much chance of cross-pollination, seeds were collected from the following species, stratified, and grown in the greenhouse: *C. acuminata*, *C. acutifolia* var. *villosula*, *C. adpressa*, *C. adpressa hessei*, *C. adpressa* var. *praecox*, *C. ambigua*, *C. apiculata*, *C. bullata*, *C. bullata* f. *floribunda*, *C. dielsiana*, *C. divaricata*, *C. foveolata*, *C. frigida*, *C. horizontalis*, *C. integerrima*, *C. lindleyi*, *C. lucida*, *C. microphylla*, *C. moupinensis*, *C. nitens*, *C. obscura cornifolia*, *C. racemiflora* var. *desfontaini*, *C. racemiflora* var. *soongorica*, *C. racemiflora* var. *veitchii*, *C. rosea*, *C. simonsii*, *C. s.* var. *newryensis*, *C. tomentosa* and *C. wardii*.

In connection with this part of the work I wish to thank Dr. Karl Sax, who helped collect the seeds, and Mr. Lewis Lipp, Jeanette Renshaw and Dorothy Thorndyke for growing and caring for the seedlings. I thank George Graves, who grew additional seedlings from three of the same seed sources and furnished the data that are also included in the table (Table II). These include 25 seedlings of *C. apiculata*, 1000 of *C. dielsiana*, and 200 of *C. divaricata*.

TABLE II
APOMIXIS IN COTONEASTER

Species	Chromosome Number	Number of Seedlings	Number of Maternals	Number of Variants
<i>C. acuminata</i>	2 n	11	4	7
<i>C. acutifolia</i> var. <i>villosula</i>	4 n	14	12	2
<i>C. adpressa</i>	3 n	6	6	0
<i>C. adpressa hessei</i>	3 n	10	10	0
<i>C. adpressa</i> var. <i>praecox</i>	3 n	4	4	0
<i>C. ambigua</i>	3 n	50	50	0
<i>C. apiculata</i>	3 n	54	54	0
<i>C. bullata</i>	3 n	14	14	0
<i>C. bullata</i> f. <i>floribunda</i>	3 n	34	34	0
<i>C. dielsiana</i>	3 n	1673	1673	0
<i>C. divaricata</i>	3 n	200	200	0
<i>C. frigida</i>	2 n	2	0	2
<i>C. horizontalis</i>	3 n	5	5	0
<i>C. integerrima</i>	3 n	44	44	0
<i>C. lindleyi</i>	3 n	16	16	0
<i>C. moupinensis</i>	3 n	21	21	0
<i>C. multiflora</i>	4 n	57	57	0
<i>C. nitens</i>	3 n	26	26	0
<i>C. obscura</i> var. <i>cornifolia</i>	3 n	16	16	0
<i>C. racemiflora</i> var. <i>veitchii</i>	3 n	13	13	0
<i>C. rosea</i>	3 n	27	27	0
<i>C. simonsii</i>	3 n	384	381	3
<i>C. wardii</i>	3 n	36	35	1

The data for this work are given in Table II. In most instances the number of seedlings from each species was not large, but most of the offspring were like the seed parent; most were maternals.

Cotoneaster acuminata and *C. frigida* showed a tendency to hybridize. They showed considerable variation in their respective progeny. Both are diploids.

The large majority of the Cotoneasters breed true. Several others did show a small percentage of variants.

Among the triploids, three of those propagated threw a small percentage of variants (Table II). Of the 26 seedlings of *C. nitens*, three were different and varying among themselves; the others were alike. One of the thirty-six seedlings of *C. wardii* varied from the type. Of 384 seedlings of *C. simonsii* all were uniform, with three exceptions. As was also true of the aberrants in *C. nitens* and *C. wardii*, the three seedlings of *C. simonsii* were conspicuously different from the others of the same species. They were striking among an otherwise uniform population. They had broader leaves which were thicker and tomentose and flattened into a rosette.

This may indicate that although *C. nitens*, *C. simonsii*, and *C. wardii* reproduced apomictically, the egg is fertilized at least at times, and that they may be crossed with other species. They are probably facultative apomictic species, as *Malus sargentii* is among the apples.

On the triploid *C. tomentosa* (Ait.) Lindl. destyled ovaries developed in about the same proportion as on the controls on other branches of the same shrub. This was also true of the destyled ovaries of the triploids *C. dielsiana* Pritz., *C. nitens* Rehd. & Wils., *C. froebellii* — a plant from Vilmorin — and *C. zabeli* Schneid., but further work along this line would be necessary before settling this point on these grounds, except for a few species. Many species so treated gave negative results, but most of the negative results are not conclusive, either because not enough work was done, or because injury in the process might cause the fruit to drop (as happened most often the first year) or because no fruit was set on the controls at the same time.

Apomixis must be very general among the triploid Cotoneasters. Many species grown in the same vicinity are in bloom at the same time. The bees and other insects are attracted to them in such large numbers that cross-pollination should be the rule. Although the divisions in the pollen mother cells were very irregular in the triploids, and often with the loss of chromatin, there was an abundant production of fruit and a great uniformity among the progeny where they were tested. This seems to establish rather definitely the presence of apomixis in the triploids.

The tetraploids were more regular in the divisions in their pollen mother cells. Seedlings of only two tetraploids, *C. acutifolia* var. *villosula* and *C. multiflora*, were grown. Among fourteen seedlings of the former two variants appeared. All were uniform in *C. multiflora*. Abundant fruit set on the plant, which was in the midst of many other species.

There is no doubt about apomixis in the triploid Cotoneasters, and it

is possible that it may exist in some of the diploids and tetraploids. There is also some evidence that some of the triploids are facultative apomicts, since three produced a small percentage of variant seedlings. It is possible that variants in other triploid species might be found if larger numbers of progeny were grown or if the triploids were hand-pollinated with pollen from triploids.

The meagre evidence of facultative apomixis in *Cotoneaster* is supported by the breeding behavior of the closely related genus *Malus*. *Malus sargentii* is found in diploid, triploid, and tetraploid forms (K. Sax unpublished). When open pollinated all produce only maternal progeny, even though they are surrounded by other species. When artificially pollinated with pollen from other diploid species, the triploids and tetraploid *M. sargentii* forms do produce some sexual progeny, but seldom more than twenty per cent. In some cases only maternal types of progeny are produced, and in all cases these types are predominant. The mechanism of this facultative apomixis is unknown. A few triploid species of *Malus* do produce an occasional variant when open pollinated, even though the great majority of the progeny are maternals. It is possible that the same type of apomixis is present in *Cotoneaster*.

DISTRIBUTION AND RELATIONSHIPS

The geographical distribution of *Cotoneaster* in relation to the 2 n, 3 n, and 4 n chromosome numbers may offer suggestions as to the origin of some of the species. Eight of the species studied are diploids. There may be other diploids among those in which the chromosome number has not been determined. The diploids *C. frigida*, *C. microphylla*, and *C. acuminata* are found in the Himalayas; *C. conspicua* in Tibet; *C. glabrata* and *C. henryana* in the Yangtze basin in western and central China; *C. dammeri* in West Hupeh in central China; and only one, *C. acutifolia* Turcz., in North China and Mongolia.

The diploids have a limited geographical distribution, and fifty per cent of them are found in Zone 7 (Rehder); only one, *C. acutifolia* Turcz., inhabits Zone 4. Wilson (75) comments that *C. acutifolia* Turcz. was originally described from Chinese Mongolia, that it was introduced by Dr. Bretschneider from mountains near Peking, and that the typical form is absent from central and western China, but varieties are found growing in these regions.

There were a number of instances in which specimens were labeled *C. acutifolia* or a variety thereof. Some of these have been considered as natural variations. Some relatives of *C. acutifolia* Turcz. have been recognized, but the situation was complex, and much has been left to be settled in the future.

A variety, *C. acutifolia* var. *villosula* Rehd. & Wils., was recognized as a near relative. A study of the chromosome number proved it to be a tetraploid form. It is a hardy shrub occupying Zone 5 in central and western China. It grows in thickets in West Hupeh, West Szechuan, and

in the Shensi mountains, the latter bordering on the habitat of *C. acutifolia* Turcz. It may have originated through the doubling of the chromosome number of *C. acutifolia* under circumstances in the past conducive to the disturbance of the chromosome balance. Two specimens labeled *Cotoneaster* sp. grown in the Arnold Arboretum from seed collected by Dr. Rock in the Tao River Basin in western China were triploids.

A large number of species which are considered as belonging to the "acutifolia group" are triploids or aneuploids with approximately the $3n$ number. Included in this category are *C. ambigua* Rehd. & Wils., which the authors considered closely allied to *C. acutifolia* Turcz., and *C. obscura* Rehd. & Wils., which they believed resembled *C. acuminata* which grows in the Himalayas in India. They thought *C. obscura* also resembled *C. foveolata* Rehd. & Wils. of West Hupeh, which seems more probable, although there may have been earlier connections with the *acuminata* ancestors. *Cotoneaster foveolata* Rehd. & Wils. in turn closely resembles *C. moupinensis* Franch., common in the thickets of West Szechuan. These were black-fruited. *Cotoneaster bullata* Bois. and its varieties are red-fruited, and when not in fruit were mistaken for *C. moupinensis*. Further comments show close external resemblance. *Cotoneaster bullata* Bois., according to Wilson, is a relatively rare plant but is widely scattered along the edge of the zone occupied by *C. moupinensis* in West Szechuan.

At first Rehder and Wilson considered *C. tenuipes* Rehd. & Wils. as nearly related to *C. racemiflora* Koch (which is on the other side of the mountains), but they lacked the flowers. Later Rehder placed it near *C. acutifolia* Turcz., which seems more probable, as these forms are all found in West China.

These triploids that resemble *C. acutifolia* Turcz. may have come from the diploid *C. acutifolia* and the tetraploid *C. villosula*. There is also the possibility of intercrossing of *C. villosula* and its descendants with other diploids of the region, as is obvious from the geographical locations and the fact that *C. acutifolia* var. *villosula* is a facultative apomict.

Cotoneaster acutifolia Turcz. may also have contributed some of its characteristics to the flora of the North. *Cotoneaster lucida* Schlecht. was once named *C. acutifolia* Lindl. It is not easily confused with *C. acutifolia* Turcz. It has dark green leaves which are very glossy and lustrous. It has also been found to be a triploid. It grows in the Altai mountains in Mongolia in Zone 4 (Rehder), in thickets at 2000–3000 m., having a limited distribution. This is probably related to *C. acutifolia* Turcz. and may have another relative in *C. melanocarpa* Lodd.

Cotoneaster melanocarpa Lodd. is a tetraploid species which ranges from northern and eastern Europe across Siberia to central and northeast Asia. It is probable that it is another tetraploid form from *C. acutifolia* Turcz. (or even *C. acuminata*, which I doubt) which, having less competition to the north as well as the necessary vigor and better adaptability, has occupied more space than most *Cotoneasters*. It inhabits Zone 4.

Varietal forms of *C. melanocarpa* Lodd. occupy more restricted areas.

The variety *C. melanocarpa* var. *commixta* Schneid. is a 4 n species and *C. melanocarpa* var. *laxiflora* (Lindl.) Schneid. is a 3 n species from central Asia. It may have been a back cross of *C. melanocarpa* with *C. acutifolia* or a cross with *C. acutifolia* var. *villosula*.

Other diploids have contributed variation to the flora around them. *Cotoneaster acuminata* Lindl. is a diploid found in Zone 5 in the Himalayas and on the side away from China. According to Wilson (75) *C. acuminata* Pritzl in Bot. Jahrb. 29: 385. 1900 (pro parte, non Lindley) is under *C. acutifolia* var. *villosula* as a synonym. There are different as to chromosome number and they are geographically separated.

Although they are distinct species, there is some resemblance and a fairly close relationship taxonomically between *C. acutifolia* Turcz. and *C. acuminata*. They may have some common or similar ancestry in the past; at present there are very definite geographical barriers between the species.

Cotoneaster frigida Lindl., a diploid, grows in the Himalayas and is cultivated in Zone 7. Rehder (56) considers *C. affinis* and its variety *C. affinis* var. *bacillaris*, a tetraploid cultivated from Zone 7 (?) to be closely related to *C. frigida*. Bean (3), in his "Trees and Shrubs," remarks that *C. affinis* var. *bacillaris* and *C. frigida* are connected by one or two intermediates. In 1899, W. J. Bean writes in Vol. 55 of The Garden that *C. affinis* is between *C. bacillaris* and *C. frigida*. The tetraploid *C. affinis* var. *bacillaris* may have been formed by a cross between two species, one of which was *C. frigida*, or by the doubling of the chromosome number of *C. frigida*.

Cotoneaster lindleyi, a triploid, also shows affinity for this group, especially *C. racemiflora*. It is an inhabitant of the Himalayas, and is cultivated in Zone 6 (?).

Cotoneaster racemiflora (Desf.) K. Koch is considered by Rehder a very variable species. It is a triploid which ranges in Zone 4 from southern Europe, North Africa, and western Asia to the Himalayas and Turkistan. It has several varieties, var. *desfontaini* (Reg.) Zab. being the typical one, and it is a triploid. It is not found in China, but some of its varieties are found there and are more limited in distribution. *Cotoneaster racemiflora* var. *soongorica* (Reg. & Herd.) Schneid. inhabits West China, Zone 3, and *C. racemiflora* var. *veitchii* central China. These are triploids.

If the species in China are closely related to the species to the west, then a common ancestor must have given rise to those on both sides of the mountains. Its wide range makes *C. racemiflora* look like an older species. It may have come from *C. frigida*, at least as one of the parents, in which there was a doubling of the chromosomes, as is probable in *C. affinis* var. *bacillaris*, or it may have come from a cross of *C. frigida* with *C. acuminata* or an unknown or extinct species. It is apparent that there is a decided difference between the Chinese *racemiflora* species and the typical form.

That the *C. racemiflora* triploids which were grown in close proximity with other *Cotoneasters* breed true shows that apomixis is fairly common.

The seed set is very good. The wide range of these triploid apomicts shows ability to adapt to a variety of locations. *Cotoneaster rosea* shows resemblances to *C. racemiflora*. It may show both *C. acuminata* and *C. frigida* traits. It is a triploid.

Cotoneaster simonsii, first collected in the Khasia Mts. in northern India, shows some resemblance to *C. acuminata* and to *C. rotundifolia*. There is a possibility that in the past it had some common ancestry with the *francheti* group — to which it is often likened.

Several of the most attractive species of *Cotoneaster* which show various degrees of similarity inhabit West and Central China. They differ from the *acutifolia* group. Among these are *C. francheti*, a tetraploid, and the triploids *C. dielsiana*, *C. dielsiana* var. *elegans*, *C. divaricata*, and *C. nitens*. *Cotoneaster wardii*, a triploid facultative apomict inhabiting Tibet, is very closely related. *Cotoneaster dielsiana* is an apomict. *Cotoneaster zabeli*, which inhabits central China, appears to have some similar traits. It and its variety are both triploids.

The origin of this group is not clear. They are all related to the tetraploid *C. francheti* Bois. The diploid *C. dammeri* grows in central China, *C. conspicua* in W. China. There are also possibilities of having earlier species mixed with ancestors of species from the southern Himalayan groups. *Cotoneaster microphylla* extends into Yunnan. Further study of the *francheti* group is necessary in order to determine its origin.

The *salicifolia*-like group of plants from the Yangtze Basin have been a problem to the systematist. *Cotoneaster salicifolia* Franch., its varieties *floccosa* (Pritz.) Rehd. & Wils. and *rugosa* Rehd. & Wils., *C. rhytidophylla* Rehd. & Wils., *C. glabrata* Rehd. & Wils., and *C. henryana* (Schneid.) Rehd. & Wils., are all evergreen or half evergreen species with prominently veined, elliptic oblong to ovate lanceolate leaves. They have attractive flowers and fruit.

Exell (17) remarks, "I am following the conclusions of Dr. Stapf (Bot. Mag. t. 8999) that *C. henryana* Rehd. & Wils. and the earlier *C. rugosa* Pritz. ex Diels are synonymous." These plants do resemble each other closely, but Rehder & Wilson (56) recognized some differences, and the study of the chromosome numbers indicates that they were correct. *Cotoneaster glabrata* and *C. henryana* are diploid species (Rehder Zone 7 ?). *Cotoneaster salicifolia* comes from Zone 6 (?). Its chromosome numbers have not been determined with certainty. Its variety *C. salicifolia* var. *rugosa* is a triploid from Zone 5.

It may be noted from the zones in which these species are found that they are fairly tender plants. Except *C. rhytidophylla* Rehd. & Wils. they are all growing in the Arnold Arboretum (in fairly protected areas) in Zone 4.

It is not surprising that Thomas (72) remarks, "If these plants are raised from seeds variation results." There are some diploids, *C. glabrata* and *C. henryana*, and some triploids. There may be facultative apomicts in some of this group.

Included by Rehder as a nearly related species is *C. glaucophylla*

Franch. inhabiting West China (Zone 7) which is also a triploid. He calls attention to some resemblance to *C. zabeli*. *Cotoneaster zabeli* is a triploid from central China. A variety, *C. zabeli* var. *miniata* Rehd. & Wils., is a triploid from central China.

The *microphylla* group, mostly prostrate plants, inhabits the Himalayas. E. H. Wilson (75) remarks that it is not seen in China, although it has been reported from Yunnan. These plants are reported to show variation in their seedlings. *C. microphylla* is a diploid. There are several *microphylla* varieties with closely related species, as *C. congesta* Bak. (Himalayas). Rehder mentions *C. conspicua* Marquand, a diploid, as a closely related species. It inhabits West China and Tibet.

It may be noted from the foregoing that the triploids vary more as to range and habitat. Some of them are as limited as the diploids, being reported from only one vicinity. Nineteen out of about forty triploids are reported from West China, four from the Himalayas, and six from Central and West China. Four more are described from Central China, two from North China, and one, *C. multiflora granatensis*, from Spain. All of these show a narrow range.

There are a few more widely ranging triploid species. *Cotoneaster integerrima* Med., an early recognized *Cotoneaster*, is a triploid which is common to Zone 5 in Europe, in the western Himalayas, and in northern Asia to the Altai Mountains in Mongolia. It has been reported from southeast Tibet and Shantung, far from any others that have been reported. Rehder collected it for the Arnold Arboretum in the Savoyan Alps in France, and Anderson collected it in the mountains in Bulgaria. Rehder considers *C. uniflora* Bge., growing in the Altai Mountains, as a closely related species, but comments that it may be only a variety of *C. integerrima*. *Cotoneaster sylvestris* of central China is also mentioned as a closely related species. *Cotoneaster zabeli* of western China shows some characteristics of *C. integerrima*.

Cotoneaster tomentosa (Ait.) Lindl. is somewhat more limited in its distribution. It grows in northern and eastern Europe and western Asia. It has been reported from Kansu. It is considered related to *C. integerrima*, but it is larger and more intense in every detail. It is a vigorous apomictic triploid. *Cotoneaster tomentosa* leaves are more like those of the *affinis* group but heavier and more tomentose; these species differ in fruit and inflorescence.

Another widely distributed triploid, *C. racemiflora*, is found growing from North Africa throughout southern Europe and western Asia to the Himalayas and Turkestan. It is reported at Tomsk in Siberia. J. F. Rock remarks that the typical *C. racemiflora* (Desf.) K. Koch is not found in China, but well-marked varieties are found in Hupeh and Szechuan. The McClaren collectors found *C. racemiflora* var. *veitchii* in the Purple Mountains near Nanking. The variety *C. racemiflora* var. *soongorica* has been collected in West China, Shantung, and Shansi.

Of the large number of triploids only two, *C. glaucophylla* and *C. wardii*, are found in Zone 7 (both questioned); six are in Zone 6, and *C. racemi-*

flora var. *soongorica* is in Zone 3. The remaining triploids in which the chromosome numbers were determined were either varieties or unknown species.

The tetraploids, which are few in number, also vary in the breadth of their distribution. *Cotoneaster acutifolia* var. *villosula* is a tetraploid from central and western China in Zone 4. *Cotoneaster affinis* var. *bacillaris* inhabits Nepal (Zone 7), *C. francheti* western China (Zone 6 ?). *Cotoneaster melanocarpa* ranges in Zone 4 from northern and eastern Europe and the Caucasus to central Asia (having been reported from Tomsk), from Turkestan through Siberia to northeast Asia in Mongolia, Manchuria, Chili and Kansu. The variety *C. melanocarpa* var. *commixta* has a more limited range. *Cotoneaster multiflora* is found in West China. *Cotoneaster melanocarpa* has the widest range of the Cotoneasters except the triploid *C. racemiflora*.

Some of the polyploids show a tendency to adapt themselves over a wider range geographically. The diploids are limited in their range. There is also a slight tendency for the diploids to be more limited zonally, about half being in Zone 7.

All European species so far studied are polyploid. They probably originate from the Himalayan species. No diploids are found in Europe, and all European species show resemblances to those of central and northern Asia. *Cotoneaster multiflora* var. *granatensis* from Spain is supposed to be related to *C. multiflora* from western China. It might, however, be related to *C. racemiflora*, which is not so far apart from *C. multiflora* in distinguishing characteristics. Its leaf pubescence is characteristic of *C. racemiflora*, being one of the characters separating the two species.

When the chromosome number and the tendency to be evergreen were considered at the time of leaf drop there was found to be a slight tendency on the part of the $2n$ species to be more evergreen and therefore more subtropical. There were deciduous diploids, *C. acutifolia* and *C. acuminata*. There were many polyploid evergreens. Some of the plants, both diploid and polyploid, were partially evergreen.

VARIATION AND EVOLUTION

Cotoneaster has long been recognized as a taxonomically difficult genus. Wilson (75) in discussing the similarities of the black-fruited Cotoneasters from China wrote "with *C. acutifolia* Turcz. at one end of the chain and *moupinensis* Franchet at the other, it is almost possible with the material before us to connect the series." As in *Hieracium*, *Crataegus* and *Rubus*, the species and varieties are often separated by minute, but constant differences.

Hybridization is still a prominent factor in the variation and evolution of the Cotoneasters. There is clear evidence of hybridization of the diploid species, both in nature and under cultivation. There is some indica-

tion of crossing between a few of the tetraploids. It is also probable that many, if not most, of the triploids were derived from crosses between diploids and tetraploids. Even some of the apomictic triploids may occasionally hybridize with diploids, as is known to be the case in *Malus*.

Although the great majority of the species of *Cotoneaster* are apomictic triploids, there are some variants among the progeny of some species. Such variation could be caused by occasional sexual reproduction, or it could be the result of internal segregation if the progeny are from unreduced egg cells, as Haskell (34) has suggested for apomictic species of *Rubus*. The meiotic irregularity and loss or non-disjunction of chromosomes could also lead to variant aneuploids, as has been suggested by Stebbins (68). There is some evidence of aneuploidy in a few *Cotoneasters*, although exact chromosome counts were not possible.

In the triploids the meiotic divisions are irregular, as may be expected, but some species are more irregular than others, with bridges found at anaphase. Although the division process is typical for each species or variety, there is much variation between the species, and due to various degrees of adherence of the homologues, the exact chromosome number is sometimes uncertain. Some of the species may be aneuploid with slight differences in chromosome number; some of the chromosomes may be lacking, but this has not been established.

Perhaps these more irregular triploids are from crosses between distantly related diploids and tetraploids which differ in chromosome structure and result in inversion bridges in the triploid hybrids. The more regular triploids may be autopolyploids between closely related forms. At any rate, the triploids do seem to fall into several rather distinct groups in respect to meiotic behavior.

Polyploidy within the species would also account for some variation since it is known that induced tetraploids are often of a stiffer habit and have larger and more deeply colored flowers than their diploid ancestors. It is just this type of variation that differentiates many of the species and varieties of *Cotoneaster*.

The variation produced by hybridization and polyploidy is "fixed" by apomixis. Although, as Müntzing and others have found, apomixis is not confined to polyploids, it does permit cytologically and genetically heterozygous species to be perpetuated. Slight variations can be maintained in "Clonal Species," a term proposed by Darlington (10).

Apomixis in polyploids permits the constant reproduction of a hybrid which would normally be sterile and would have little survival value. Yet it is known that many artificially produced triploids which must be propagated by grafts or cuttings are superior to either the diploid or tetraploid parent in vigor and in horticultural value (K. Sax unpublished). The fact that most of the species of *Cotoneaster* are apomictic triploids shows that they have high survival values and can be easily propagated.

The polyploid species of *Cotoneaster* do have a wider range of distribution than the diploids. The diploids are largely confined to the Himalayas, West and Central China, while some of the triploids and tetraploids are widely distributed. The triploids *C. racemiflora*, *C. integerrima*, and *C.*

tomentosa have occupied a wide territory. *Cotoneaster lucida*, although limited in distribution, has adapted itself to a colder zone. The tetraploid *C. melanocarpa* has spread over large areas from northern and eastern Europe through Siberia and Manchuria. These widely distributed species are polyploid apomicts.

Excessive uniformity brought about by apomixis might be a handicap, even though under original conditions the triploid or hybrid apomictic species may have definite advantages and greater adaptability. As Stebbins (68) has suggested, the uniformity imposed by apomixis would be a handicap in a changing environment, and the lack of variation would be a block to further evolution.

In *Cotoneaster*, however, there is occasional variation in the progeny of apomictic species. These species still have some plasticity to meet a changing environment, either through occasional sexual progeny, internal segregation, or chromosome irregularity. Thus they have the ability to perpetuate an unbalanced cytological and genetic complex of adaptive value and yet have the capacity to produce variants to meet new environmental conditions.

Polyploidy and hybridization provide most of the variation in *Cotoneaster*. Often the differences are slight, yet they are fixed by apomixis, providing distinct variants which reproduce true to type. Some of these may have a wide distribution. It is this complex of variation due to polyploidy and hybridization, combined with apomixis, that makes the genus *Cotoneaster* a difficult one for the taxonomist. For the horticulturist apomixis is an advantage, since most of the ornamental species and varieties breed true from seed.

SUMMARY

The chromosome numbers were determined in forty-one species and eighteen varieties of *Cotoneaster*. Of these *Cotoneasters* eight taxa were diploid, forty-three triploid, six tetraploid, and two polyploids could not be determined. Some aneuploidy may be present, as several triploids seem to vary.

Progeny from twenty-three species show that two diploids reproduced sexually. The rest reproduced apomictically, an occasional variant appearing among three of the nineteen triploids: *C. nitens*, *C. simonsii*, and *C. wardii*. One tetraploid was a facultative apomict.

The diploids are limited in their geographical distribution, as are most of the triploids and tetraploids. Among the triploids three species, *C. integerrima*, *C. racemiflora*, and *C. tomentosa*, show wide distribution. One tetraploid, *C. melanocarpa*, is found over wide areas. The diploids showed a slight tendency toward zonal, as well as geographical limitation.

Apomixis stabilizes a species, but the genus *Cotoneaster* is given flexibility through sexual reproduction and through facultative apomixis. There are probably some obligate apomicts, i.e., *C. dielsiana*.

Apomixis and polyploidy are responsible for the taxonomic complexity of the genus *Cotoneaster*.

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